A.R. Sen

A review of some important techniques in sampling wildlife

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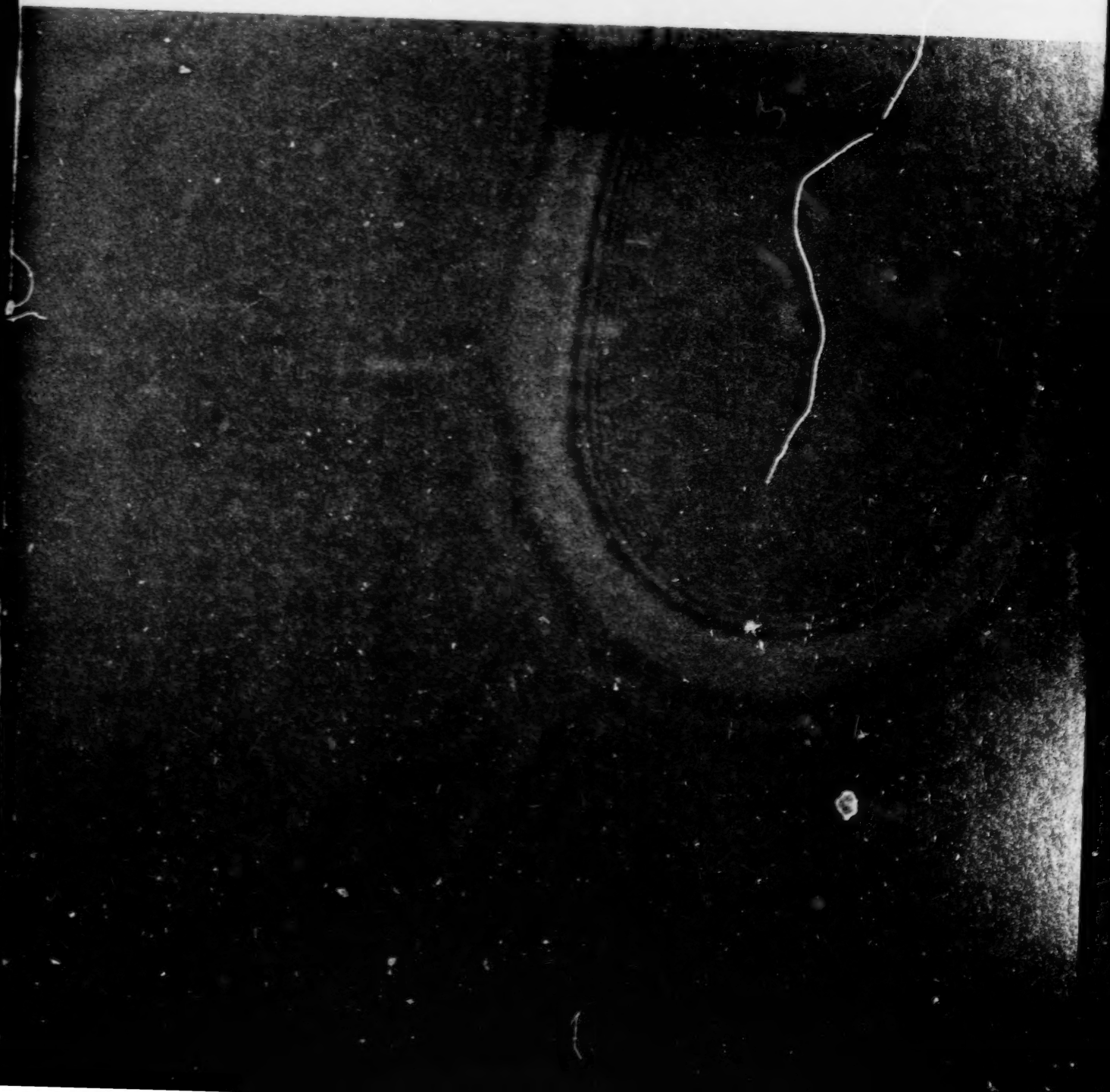

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Abstract

This paper reviews some of the important methods for estimating animal numbers or densities based on (*i*) direct counts of population units as used in quadrat, strip, line-transect, and line-intercept sampling and (*ii*) indirect counts and indices, such as capture–mark–recapture, change-in-ratio, and catch–effort methods, and indices based on track, call, roadside, and pellet-group counts.

Introduction

Wildlife managers must determine population size or density of a species in a given area and monitor changes. They must know the absolute population of each species in order to inventory game animals, to list the effects of management processes, to regulate the harvest by hunters, and to study the relations of various species within the community. Animals are harder to count than plants because animals often hide from us or they move so fast that the same individual may be counted repeatedly or not at all. This paper surveys the sampling techniques commonly used to gather data for management decisions and deals mainly with the estimation of population totals and ratios.

Ducks in a trap for capture-mark-recapture studies
Photo: S. Wendt

Wildlife sampling methods

Basically the methods of estimating animal numbers or densities can be divided into two categories: those based on direct counts of population units, and those based on indirect counts and indices.

Generally it is essential to estimate population size by a sampling method adapted to the particular species, time, place, and purpose. Careful definition of the population of interest is required so that the relation of the primary sampling unit to the population of interest is understood. Careful planning is essential to develop a workable sampling technique that will stay within budgetary constraints of time and resources and produce estimates with sufficient accuracy to be useful in making management decisions.

Because much information on sampling estimates and their errors is available in the sampling literature, I will describe only those procedures having special application to wildlife. In another paper, I will review measurement errors (which are less known but play an important role) and, where possible, indicate methods for controlling them. What follows is a summary of some of the important methods for estimating animal numbers and their sampling errors based on direct counts, such as quadrat, strip, and transect sampling; and methods based on indirect counts, such as capture–mark–recapture, change-in-ratio, and catch–effort statistics, and indices that are related in a numerical way to the animal, such as counts of calls, and roadside and pellet-group counts. The indices or ratios do not provide estimates of absolute populations, but they do indicate trends in population over years and habitats.

1. Quadrat sampling

Quadrat sampling is a procedure used usually to sample populations when a population frame is not available. Quadrat sampling is the preferred technique for most big game surveys. It is often, but not exclusively, used to investigate the spatial distribution of a population. Usually, the quadrats are small, and evenly placed in the small area that is to be sampled. Often the quadrats are designed so that the population units within them are as homogenous as possible. A known number of quadrats are randomly chosen, and the population units within each quadrat are counted.

Quadrat size and shape will depend upon the habitat, abundance, and mobility of the species. When a population is randomly distributed, the size of the quadrat will not affect the variance because the variance of a Poisson series is equal to its mean. Hence the size of a quadrat should be sufficient to give as random a distribution as feasible. Also, in such a case, the number (s) of quadrats to be sampled is given (Seber 1973) by:

$$s = \frac{S}{1 + NC^2} \tag{1}$$

where S is the total number of quadrats and N is the size of the population being sampled and C is the coefficient of variation of $\hat{N}$. A large number of quadrats will have to be sampled to provide reasonably precise estimates when N is small.

Often animals, such as small mammals, tend to congregate in shelters so that the population is not randomly distributed. In particular, if the distribution is negative binomial, with parameters P and K, the number of quadrats (s_1) is given by:

$$s_1 = \frac{1}{C^2}\left(\frac{S}{N} + \frac{1}{K}\right) \tag{2}$$

where $K > 0$.

It is obvious that $s_1 > s$, so that a larger number of quadrats of the same size and shape will have to be sampled (than is needed for a random distribution) to estimate N with the same precision.

In selecting the quadrat size, consideration must be given to edge effects. In small quadrats the ratio of edge to area increases, so that there is a greater chance of error per unit area in determining whether individuals on the edges of the quadrat are inside or outside the boundary. However, this error, which is generally positive, may not be too serious in big game aerial counts because other visual biases tend to underestimate the animals present.

When population density is known to vary over different areas, either very small or large quadrats are recommended (Greigh-Smith 1964). Also, in such cases, stratified sampling is more efficient than simple random sampling. To estimate elephant populations in the Mkomazi region of East Africa, Watson *et al.* (1969) divided the region into areas of high and low elephant density by reconnaissance flying over the whole region. Often the variance varies greatly between strata as for many clumped species (e.g., high density strata generally have greater variance than low density ones). In such cases, optimum allocation based on variance estimates will generally result in greater precision than allocation proportional to strata sizes. Siniff and Skoog (1964) used stratified quadrat sampling with optimum allocation of sampling effort in aerial surveys of Alaska caribou; this method reduced variance by more than half over that of simple random sampling. Another approach, which is generally easier and quicker to implement in the field, is to subsample a sample of strips or select one or more systematic samples of strips. Where it is difficult or time consuming to count all animals in all the sampled quadrats completely, two-phase

sampling using ratio or regression methods may be adopted. Suppose we wish to estimate the number of beavers in a tract of forest. Determining the number of resident beavers in a quadrat may require prolonged observation. However, counting only the number of beaver lodges per quadrat is straightforward and the number of lodges can be estimated for the tract from a preliminary sample of quadrats. Also, the ratio of number of beavers to total beaver lodges can be estimated from a second-phase sample or subsample of the quadrats. The two estimates can be combined to obtain the number of beavers in the tract.

Cook and Martin (1974) and Cook and Jacobson (1979) proposed improvements in the quadrat sampling method used in aerial surveys by developing models for estimating the magnitude of visibility.

2. Strip transects

Strip-transect sampling can be used to sample large areas when a population frame is not available. All the animals within a strip of fixed width are counted (we assume they have a known and equal probability of being observed). When the objects being censused are fairly numerous and readily visible, the strip-transect may consist of a long and narrow plot or quadrat. Parallel lines one strip width apart determine the population of strips. A sample of strips is composed of randomly chosen strips from the population of strips. Most of the sample surveys of marine mammals have utilized strip transects. A strip of a specific width is searched from the air or from a ship, and only those animals observed within the strip are tallied. The estimate of the total is given by $\hat{N} = n/\hat{p}$ where n represents the observed count within the strip and $\hat{p}$ is the average probability of seeing a mammal given that it falls in the strip. For any fixed point within the strip censuses, McLaren (1961:164) gave the probability that an animal will be observed as $p = (t + s)/(s + u)$ where s is the time a mammal spends on the surface, u is the time spent submerged and t the duration of the period when a submerged mammal would be visible to an observer. Eberhardt (1978) provides a derivation of the probability. The probability has two components, one being the probability $[s/(s+u)]$ that an animal will be on the surface when it comes within sighting range and the second, the probability $[t/(s+u)]$ that a submerged animal will be visible while in range. McLaren derives an average probability of sighting from the expression for p on the assumption that any sighting angle will be equally likely to occur. Eberhardt *et al.* (1979) discuss some of the practical difficulties involved in this and other methods for estimation of marine mammals.

In situations where population areas are irregular in shape either simple random or PPS (probability proportional to size) can be used to choose the strips. An observer walks the length of the strip and records the number of animals (or birds) seen. All animals in the strip are assumed to be counted. Efficiency of the design will be increased if the lines are parallel to the direction of greatest ecological change. Strips of varying length can be chosen by selecting pairs of co-ordinates at random. Jolly (1969) adopted PPS selection with replacement so that when a strip happened to contain n (more than one) sample points it was counted n times in estimation, although it was surveyed once only. Longer transects, therefore, receive a greater weighting than shorter ones in the estimation of the population total. Jolly was concerned mostly with situations involving sampling fractions of 5% or less.

A number of aerial surveys on wildlife utilized strip transects instead of quadrats, because strip surveys are usually easier to conduct and they involve less risk of double counting or missing animal groups due to (*a*) difficult terrain and (*b*) movement of animals. Such surveys are generally more efficient than surveys on large quadrats and are more convenient to position given a baseline running across the population area.

3. Line-intercept and line-transect methods

Both the line-intercept and the line-transect methods are sampling procedures that do not depend on the availability of a natural frame. The line-intercept method, which is useful for estimating inanimate objects with varying size (e.g., shrub canopies or den sites of animals), consists of choosing a transect of length L at random (Fig. 1) in an area (say, $L \times W$), measuring the length of the transect intersected by each member of the population to estimate the population total in the given area. In line-intercept sampling the probability that an object is sampled is proportional to a measure of length of the object and the technique consists in replacing each object on a map by a "needle" (e.g., Fig. 1: w_1, w_2, w_3) so that the sample would consist of all objects whose needles intersect the transect line. If w_i is the width of a shrub canopy parallel to the base line W intersecting a random transect, and if m is the total number of elements, e.g., shrubs or den sites intersecting n randomly selected transects, unbiased estimates of the population total and its variance are given by the following:

$$\hat{N}_I = \frac{1}{n} \sum_{i=1}^{m} \frac{1}{p_i} \tag{3}$$

$$v(\hat{N}_I) = \frac{1}{n^2} \sum_{i=1}^{m} \frac{(1-p_i)}{p_i^2} \tag{4}$$

where $p_i = w_i/W$. De Vries (1979*a*) provides a good review of the subject and develops the methodology for line-intersect subsampling for dense populations where a number of elements may happen to intersect the sampling lines. Seber (1979) notes that random distribution of the elements is not necessary for arriving at (3) though this is required for deriving (4). For non-random distributions, variance estimates are best obtained by the use of replicated subsampling (Sen *et al.* 1978). Line-intersect sampling has been discussed by McIntyre (1953), Warren and Olsen (1964), Wagner (1968), De Vries (1973, 1974, 1979*a*, 1979*b*), Eberhardt (1978), Seber (1979), and others. Line-intercept sampling is a special case of "length-biased sampling" (Cox 1962, 1969) and "size-biased sampling" (Schaeffer 1972), terms coined to characterize procedures in which the probability of sampling a particular element in a population is proportional to some dimension of the element.

The line-transect method is generally used to measure the number of large terrestrial mammals or birds in a specified area. When the objects are either rare or not readily seen or both, use of fixed width as in strip transect sampling would not only be biased in the sense that in some of the transects all the objects may not be countable but also uneconomic because a large number of transects would have to be included to provide reasonably reliable estimates. In such a case, it is preferable to adopt the line-transect method, which utilizes data on all objects seen on either side of a transect line for estimating the "effective width" W of the strip covered by the observer as he or she moves along the transect line. Different methods proposed for estimating the

Figure 1
The line-intercept method of wildlife sampling

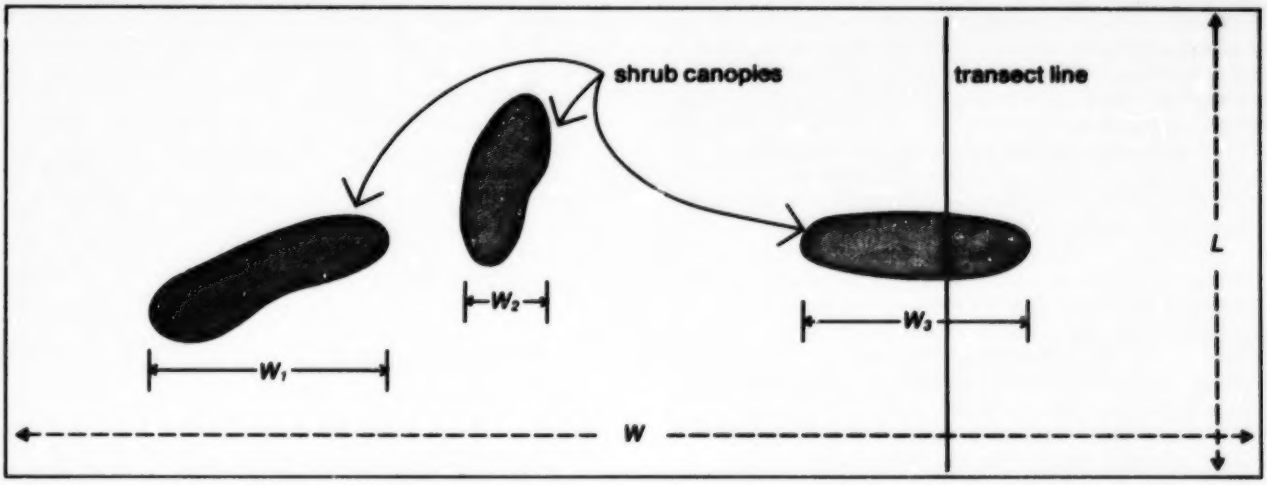
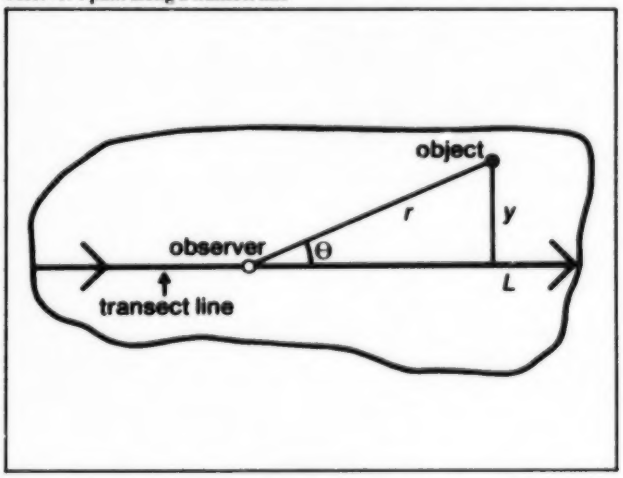


Figure 2
The line-transect method of wildlife sampling. The arrow shows the observer's path along a transect line



population total are of the form $N = AD$ where D, the population density, is estimated by

$$\hat{D} = \frac{n}{L}\left(\frac{\hat{1}}{W}\right).$$

Anderson and Pospahala (1970) propose a line-transect method to estimate the "effective width" due to lack of visibility of all duck nests within the strip. Burnham and Anderson (1976) propose using an estimate of frequency of observations directly on the transect line.

In line-transect sampling (Fig. 2), an observer estimates the population size N by walking a fixed distance L across a tract of area A in non-intersecting and non-overlapping lines or transects and records the number of animals (n) observed, the right angle distance (y) from the point where the animal is flushed to the transect line, and the radial distance (r) from the animal to the observer.

For estimating population total or density, Eberhardt (1968) proposed two basic models (*i*) with fixed flushing distance (Hayne 1949), and (*ii*) with variable flushing distance in which the instantaneous probability of flushing is assumed to be a function of the distance between the observer and the animal. Burnham (1979) has generalized the Hayne (1949) model by using an elliptic model for animal detection. Gates *et al.* (1968) and Gates (1969) have developed variable distance models for estimating population total and its error based on the assumption that the right angle flushing distance y follows an exponential distribution (density: $\lambda e^{-\lambda y}$, $y > 0$).

Sen *et al.* (1978) consider estimators based on the gamma distribution. If the population area is irregular and transect lines run right across it, the length of a randomly selected transect will be a random variable (Seber 1979). Seber (1973) considers a more general model than that of Gates and Eberhardt and lists seven assumptions underlying the various models. He also suggests methods for testing some of the assumptions. Ramsey (1979) states that the main problem of estimating density in parametric models is to estimate the effective width of the area that the observer surveys. Effective width appears as a scale parameter in the distribution of detection distances. Eberhardt (1978), Gates (1979), and Burnham *et al.* (1980) provide excellent reviews on the subject. Burnham *et al.* (1980) state the most critical assumptions as follows: (1) if an object is on the transect line, the probability of its being seen is unity, (2) when flushed, each animal is seen at the exact position it occupied when startled by the observer's approach and no animal is counted more than once, (3) distances and angles are free from measurement errors, and (4) the sighting of one animal is independent of the sighting of another.

Assumption (1) may not always be true, e.g., in aerial surveys, the probability of sighting an animal on the transect line is not unity. Burnham *et al.* (1980) cite, as examples, burrowing animals which violate the assumption. Investigation is needed into the bias resulting from a breakdown of this assumption. Assumption (2) is generally violated by wildlife populations which tend to move away to avoid the observer, who consequently either misses the animal or sees it after it has begun to move and measures the perpendicular distance from the wrong spot. Seber (1973) suggests that as long as the animals missed represent a constant proportion the estimate will still be valid. Smith (1979) proposed a model

for estimation when the assumption that "the animals are immobile before detection" is violated.

To obtain precise estimates of population, flushing distances must be measured as accurately as possible. In practice, an estimator based on radial distances (Hayne 1949) would be preferable because the relative error in measuring radial distances should be less than that for right angled distances. Assumption (4) is often violated (Sen *et al.* 1974) in practice, e.g., Ruffed Grouse (*Bonasa umbellus*) which tends to flush in pairs. This will, however, not affect the unbiasedness of the estimates, though it will tend to increase the variance of the estimates.

Seber (1973) pointed out that one of the main problems in the use of line-transects is the choice of the appropriate model. For this, it is necessary that data be recorded separately for each segment of length l (L/s) where s is the number of transects. This is essential if the sample mean and variance (estimated from s repeated samples) are to be compared with the theoretical mean and variance.

Cox (1969) developed a non-parametric method for obtaining unbiased and biased (with lesser mean square error) estimates of density. Burnham and Anderson (1976) describe a general theory for non-parametric estimation of line transects by fitting a smooth curve to the midpoints of a frequency distribution of right-angle sighting distances and then using the curve to estimate density. Gates and Smith 1980) propose a specific algorithm for fitting a polynomial of degree m to the midpoints of a frequency histogram.

Ramsey and Scott (1979) examine non-parametric methods for estimation of population densities from line-transect surveys using variable circular plots.

The non-parametric method poses some special problems in variance estimation. One of the methods of estimating variance of density or total is the use of replicated subsamples (Sen *et al.* 1978). The method amounts to making a number of independent estimates of the overall total, each based on an independent random subsample of transect lines. The variance estimate for the survey is then calculated from the variance of the independent estimates.

4. Capture – recapture method

In this method M individuals from a population are caught, marked, and released. On a second occasion, a sample of n individuals is captured. If m be the number of marked animals in the sample, a biased estimate $\hat{N}_2$ of the population size N and a biased estimate $v(\hat{N}_2)$ of its variance are as follows:

$$\hat{N}_2 = \frac{n}{m} M \tag{5}$$

$$v(\hat{N}_2) = \frac{\hat{N}_2^2 (\hat{N}_2 - M)(\hat{N}_2 - n)}{Mn(\hat{N}_2 - 1)} \tag{6}$$

Petersen (1896) used this method in his studies of the European plaice (*Pleuronectes platessa*) and Lincoln (1930) later proposed it for estimating the number of ducks. Kabat *et al.* (1953) employed the Lincoln Index in estimating deer numbers in Wisconsin. The method was extensively reviewed by Cormack (1968, 1979), Seber (1973), Otis *et al.* (1978), and others. The estimate $\hat{N}_2$ is based on certain important assumptions, (*i*) the population is closed, i.e., N is constant, (*ii*) all animals have the same probability of being caught in the first sample, (*iii*) capturing and marking do not affect the survival of the animals involved, (*iv*) any marked animal has the same chance of being captured as an unmarked one in the second sample, (*v*) marks are not lost in-between the two samples, and (*vi*) all marks are reported on recovery in the second sample.

The decline in the proportion of tagged rabbits in the kill as the hunting season progresses at Michigan's Roselake Wildlife Experiment Station (Peterle and Eberhardt 1959) is a violation of assumption (*iv*). Otis *et al.* (1978) have considered a number of models and estimators for closed populations when assumption (*iv*) is not met as a result of capture probabilities varying over (*a*) time, (*b*) capture history (behaviour), and/or (*c*) individual animals.

When $n + M \geq N$, Chapman (1951) proposed an unbiased estimator

$$\hat{N}_3 = \frac{(M + 1)(n + 1)}{(m + 1)} - 1 \tag{7}$$

based on the hypergeometric distribution.

Seber (1970) provided an unbiased estimate of its variance:

$$v(\hat{N}_3) = \frac{(M + 1)(n + 1)(M - m)(n - m)}{(m + 1)^2 (m + 2)} \tag{8}$$

Bailey (1951, 1952), using a binomial approximation to the hypergeometric distribution obtained the maximum likelihood estimator (MLE) of N which is the same as the Petersen estimate. Because the coefficient of variation (C.V.) of $\hat{N}_2$ is approximately given by $1/m^{1/2}$, it follows that for the Petersen estimate to be efficient, we should have sufficient recaptures in the second sample. A closer examination of (6) will, however, show that the precision of the estimate $\hat{N}_2$ will also depend on M/N and would increase with increase in the proportion marked. Bailey (1951) discusses the use of inverse sampling with Petersen's censuses, i.e., a procedure in which the second sampling proceeds until the number of marked animals (m) is recovered.

In this method, for a given C.V., which is approximately given by $\{(M - m + 1)/[m(M + 2)]\}^{1/2}$, m can be chosen beforehand to give this desired value of C.V., M being known. Thus, if $M = 100$ marked birds, and a C.V. of 10% is desired for the estimated population size, sampling must continue until $m = 50$ marked birds have been caught. Inverse sampling usually results in more precise estimates of population size than direct sampling (Chapman 1952), though it may be inefficient per unit cost and in the absence of any information about N.

Researchers frequently mark and recapture individual animals on a series of occasions; the individuals that are unmarked when caught are marked and returned to the population. When the number of marked animals is negligible relative to the total population, Schnabel (1938) has suggested extension of $\hat{N}_2$ when marking is being carried on over a period of time. Her formula is as follows:

$$\hat{N}_4 = \sum_{i=2}^{T} n_i M_i \Big/ \sum_{i=2}^{T} m_i \tag{9}$$

which is an approximation to the solution of the equation

$$\sum_{i=2}^{s} \frac{(n_i - m_i)}{(N - M_i)} M_i = \sum_{i=2}^{s} m_i \tag{10}$$

where n_t = total sample collected at t^{th} time, M_t = number of marked individuals in population just prior to taking sample at t^{th} time, and m_t = number of marked individuals collected in sample at t^{th} time. It is easy to see that $\hat{N}_4$ is a weighted average of the Petersen estimate ($n_t M_t / m_t$). Schnabel did not provide a measure of precision of the estimate.

Chapman (1952) showed that the MLE of N is the solution of the equation

$$\prod_{i=1}^{s} \left(1 - \frac{n_i}{\hat{N}}\right) = 1 - \frac{M_{s+1}}{\hat{N}} \tag{11}$$

where M_{s+1} is the number of different individuals seen during the experiment. An estimate of the mean square error of this estimate given by Darroch (1958) is

$$\left[\frac{1}{\hat{N} - \rho} + \frac{(s-1)}{\hat{N}} - \sum_{i}^{s} \frac{1}{\hat{N} - n_i}\right]^{-1} \tag{12}$$

where $\rho = E(M_{s+1})$. Darroch and Ratcliff (1980) provided a new estimate of the size N of a closed population when s random samples, each of size one, are taken from a closed population of individuals. The new estimate is easy to calculate and although not sufficient for N is shown to have a high asymptotic efficiency. Sen and Sen (1980) deal with the theory and application of five estimators of population size (N) based on large samples for closed populations and for given multiple-capture occasions with varying capture probabilities.

Equation (5) implies that recapturing is done before there is any mortality, immigration, or emigration, i.e., assumption (*i*) holds. Robson and Flick (1965) provide a non-parametric test for detecting and eliminating recruits. It is difficult to suppose that assumption (*ii*) will hold, because of an inherent variation in catchability between subgroups, by age, sex, species, etc., so that the more catchable ones are caught in the first sample and hence more likely to be caught in the second sample thus violating assumption (*iv*) which may lead to serious bias in the Petersen estimate. Robson (1969) provides a test of the randomness of the second sample which may be violated due to animals being trap-shy or trap-happy. Some of the important references are rats and voles (Chitty and Shorten 1946), squirrels (Evans 1951), and rabbits (Geis 1955), Edwards and Eberhardt (1967). Marten (1970) used regression for testing the assumption and estimating the population when the probability of catching a marked animal is a constant multiple of the probability of catching an unmarked animal.

Chapman in Eberhardt *et al.* (1979) refers to a double-sampling marking scheme to adjust for loss in the estimates and provides a test for assumption (*v*). Seber and Felton (1981) investigate the effect of tag loss on both the estimates of population size and their variance for both single and double tagging; corrections for loss in double tagging are provided, assuming independence of the tags whether or not they are distinguishable. Seber (1973) provides a detailed discussion of the tests for the validity of the assumptions and of the consequences when the latter are violated.

Fisher and Ford (1947) developed a method that requires several releases and several recaptures and is based on the consideration that samples released early are exposed to natural mortality far longer than samples released at a later date. The method assumes that survival rate is constant and is more general than the Schnabel-model in which the survival rate is taken as unity.

The above methods are based on deterministic models which assume a constant survival rate over the interval. Jolly (1965) and Seber (1965) used a stochastic model for the situation in which an animal has a probability of survival over an interval and covers cases in which there are both deaths (and emigration) and births (and immigration). These generalizations are more efficient than the Fisher and Ford model when there are enough data to estimate the survival rate. However, the increase in the number of parameters that have to be estimated in the Jolly–Seber model tends to decrease the precision of the estimates (Cormack 1979). Arnason and Baniuk (1980) describe a computer system for estimating the parameters in the Jolly–Seber models. This will facilitate the lengthy computations and data manipulations involved. Manly and Parr (1968) and Cormack (1972, 1973) have proposed intuitively reasonable estimates for certain generalizations. Jones (1964) and Cormack (1968) have reviewed various extensions of the capture–recapture method. Pollock (1975) used Robson's general model to find maximum likelihood estimates for various situations in which catchability may depend on previous capture history.

Seber (1970) and Robson and Youngs (1971) developed models for a tag–recapture experiment assuming that annual survival, exploitation, and reporting rates are year-specific but independent of age. These models, however, are valid for birds banded as adults only, because young and adult birds are supposed to have different survival rates. Seber (1973) recommended that more use be made of (*a*) age and (*b*) returns from dead animals. Brownie and Robson (1976) have developed new models which admit different survival and reported exploitation rates of young birds and require that data be recorded separately for birds banded as adults and as young-of-the-year. Brownie *et al.* (1978) provide recent developments in banding and recovery analysis with special reference to migratory birds. The authors start with a discussion of assumptions and tests of 14 models and conclude with guidelines on sample size for planning future banding studies.

North and Morgan (1979) have developed models in which the survival rates for first-year herons are weather-dependent (time-specific) and the rate for second-year birds is a constant and different from the constant annual survival rate assumed for all older birds. Jolly (1979) considered a general model that leads to all observed frequencies being regarded as mutually independent Poisson variables.

5. Change-in-ratio (CIR) method

I will now describe a method for estimating size of closed populations, that is based on the change in sex ratio caused by a selective kill. The size can be estimated, knowing the original and final sex ratios, and the sex composition of the harvested catch. The sex ratio is determined before and after the kill by sampling methods. Scattergood (1954) refers to several field applications of the method. The method applies to ratios by age, size, colour, marked to unmarked, etc. Kelker (1940, 1942) first noted the method for estimating deer and other wildlife populations in which the bulk of hunting pressure was directed against the males. Chapman (1954, 1955) gave a statistical treatment of the method for closed populations and provided for the first time expressions for sampling errors of the estimates. Paulik and Robson (1969) provide a summary of the method and more recently Seber (1973) has given an excellent treatment of the method for both closed and open populations.

Consider a closed population of animals and assume that a differential in the numbers of males and females occurs before and after hunting. The information available is as follows:

n_t = size of samples taken at the beginning and end of the "harvest period" ($t = 1, 2$),
f_t = number of females in samples n_t ($t = 1, 2$),
m_t = number of males in samples n_t ($t = 1, 2$),
P_t = m_t/n_t ($t = 1, 2$) where $n_t = m_t + f_t$,
R_m = number of males caught during the harvest period (the period between times 1 and 2),
R_f = number of females caught,
R = $R_m + R_f$

We wish to estimate the following:

M_1 = number of males in the population before hunting ($t = 1$)
F_1 = number of females in the population before hunting ($t = 1$)
N = $M_1 + F_1$ ($t = 1$)

and their sampling errors.

Assuming sampling with replacement, the MLEs of N and M are, after Chapman (1954), the following:

$$\hat{N}_1 = \frac{R_m - Rp_2}{p_1 - p_2} \tag{13}$$

$$\hat{M}_1 = p_1\hat{N}_1 \tag{14}$$

F_1 is estimated by subtraction, i.e., $\hat{F}_1 = \hat{N}_1 - \hat{M}_1$
Also, the asymptotic variances of $\hat{M}_1$ and $\hat{N}_1$ are as follows:

$$\sigma^2(\hat{M}_1) = (P_1 - P_2)^{-2}\left[P_2^2\frac{M_1F_1}{n_1} + P_1^2\frac{M_2F_2}{n_2}\right] \tag{15}$$

$$\sigma^2(\hat{N}_1) = (P_1 - P_2)^{-2}\left[\frac{M_1F_1}{n_1} + \frac{M_2F_2}{n_2}\right] \tag{16}$$

where $P_t = M_t/N_t$ ($t = 1, 2$) and are estimated by substituting for P_1, P_2, M_1, M_2, F_1, and F_2 their estimates p_1, p_2, $\hat{M}_1$, $\hat{M}_2$, $\hat{F}_1$, and $\hat{F}_2$ respectively. MLEs of M_2, N_2, and F_2 can be obtained by solving equations similar to (13) and (14).

Of special interest are cases where only males are hunted, e.g., among deer when only the buck population is hunted. In this case (13) and (14) reduce to the following.

$$\hat{N}_1' = R_m\frac{(1-p_2)}{p_1-p_2},\ \hat{M}_1' = p_1\hat{N}_1'$$

Formulae (13) to (16) assume (*i*) that there is no natural mortality during the harvest period, (*ii*) all animals have the same probability of capture in the t^{th} sample ($t = 1, 2$), and (*iii*) the numbers caught R_m and R_f are known exactly. For most species of waterfowl, males are more easily seen than females during the breeding season because of behavioural differences. Similarly, in fishing for brook trout (*Salvelinus fontenalis*) and cisco (*Coregonus* sp.), the former is more vulnerable to gill nets than the latter. Hence in such cases assumption (*ii*) will be violated resulting in highly biased estimates of N_1 and M_1. However, where one of the two groups, e.g., females, is not harvested at all, R_f will be zero and both $\hat{M}_1$ and $\sigma(\hat{M}_1)$ will be robust with regard to such departures. A detailed discussion of the subject is given in Seber (1973).

Assumption (*iii*) will be false because R_m and R_f would not, generally, be known precisely because of unknown natural mortality, unreported kill such as "crippling loss" (e.g., Whitlock and Eberhardt 1956), and survey errors in estimating the total kill based on sample surveys during the hunting season. Where $\hat{R}_m$ and $\hat{R}_f$ are independent unbiased estimates of R_m and R_f, $\hat{N}_1$ in (13) and (16) may be replaced by:

$$\hat{N}_1 = \frac{\hat{R}_m - \hat{R}p_2}{p_1 - p_2} \tag{17}$$

and $v(\hat{N}_1) =$

$$(p_1 - p_2)^{-2}\left[\hat{N}_1^2v(p_1) + \hat{N}_2^2v(p_2) + (1 - p_2)^2v(\hat{R}_m) + p_2^2v(\hat{R}_f)\right] \tag{18}$$

It is easy to see that $\hat{N}_1$ will provide a more precise estimate when estimating large differences $P_1 - P_2$. Usually estimates of ratios P_1 and P_2 are based on aerial surveys or on aerial sample surveys corrected by ground surveys conducted on a subsample of the aerial survey.

Otis (1980) has extended the CIR method for estimating the size of animal populations by splitting the populations into three disjoint and exhaustive components instead of two as is currently done. He cites a situation in aerial sampling where animals could better be categorized as male, female, or juvenile rather than male or female.

6. Catch–effort method

In catch–effort method one unit of sampling effort is assumed to catch a fixed proportion of the population. The method is based on the assumptions that the number killed per year is proportional to the number in the population and that the population is closed. Seber (1973) gives an excellent review of the method for both closed and open populations. In this discussion we will consider closed populations only. Let:

N_t = population size at the beginning of the t^{th} time period,
N = initial population size,
n_t = size of the sample removed during the t^{th} time period, ($t = 1, 2, \ldots, s$)
e_t = effort applied in the t^{th} time period,
C_t = n_t/e_t = catch per unit effort in the t^{th} time period,
k_t = cumulative catch through time period $(t-1) = \sum_{i=1}^{t-1} n_i$
E_t = cumulative effort till time period $(t-1)$.

We will first consider the case using *variable* sampling effort. We will further assume that (1) units of effort are independent and additive and (2) all individuals have the same probability (p_t) of being caught in the t^{th} sample.

The joint probability of the $\{n_t\}$ is given by the following:

$$f(\{n_t\}) = \prod_{t=1}^{s}\binom{N - k_t}{n_t}p_t^{n_t}(1 - p_t)^{N-k_{t+1}} \qquad (t = 1, 2, \ldots, s) \tag{19}$$

From (19), it follows that C_t, the catch per unit effort, can be expressed by the linear regression model:

$$E[C_t|k_t] = K.N_t, \quad t = 1, 2, \ldots, s \tag{20}$$

where K is a constant (the catchability coefficient — the fraction of the population taken by one unit of effort) at all levels of effort and population size. Because the population is closed except for removal through catching we have

$$N_t = N - k_t$$

Hence (20) reduces to:

$$E[C_t|k_t] = K(N - k_t) \tag{21}$$

This result was first given by Leslie and Davis (1939) and DeLury (1947).

The values of C_t plotted against those of k_t will be a straight line with intercept KN and slope-K whence N can be estimated. DeLury (1951) noted that the linear relationship may hold even if the assumptions are not satisfied, e.g., C_t and k_t will be linearly related if a constant effort and a constant mortality rate operated throughout the sampling period.

If (21) holds, it can be shown (DeLury 1947) that the relation:

$$E(\log C_t) = \log(KN) - K(\log e)\, E_t \tag{22}$$

also holds, where log denotes logarithm to base 10 and log e = 0.4342945. Thus estimates of K and N can also be obtained, if the points ($\log C_t$, E_t) lie on a straight line.

In general (21) is preferable to (22) though both lines should be plotted as a check on the underlying assumptions. Both (21) and (22) have been extensively used in fishery work.

Consider the case where the probability of capture p_t remains constant over time periods (p) which is possible if *sampling effort remains unchanged* for each sample under almost identical conditions. In this case, apart from closure of the population, we assume that (1) the probability of capture p_t in the t^{th} sample is the same for all animals exposed to capture and remains constant for all the samples, i.e., the animals do not become trap-shy, and (2) the proportion caught each time is large enough to bring about an appreciable reduction in population size. Zippin (1956) has shown that the second requirement is necessary for reasonably accurate estimates and this is a serious limitation of the method.

For the practical case when two samples (say) may be needed if p is to remain constant during the survey period, we have for $s = 2$, $p_1 = p$ and $n_1 > n_2$, the MLEs of N and p as

$$\hat{N} = n_1^2/(n_1 - n_2) \tag{23}$$

$$\hat{p} = [(n_1 - n_2)/n_2] \tag{24}$$

Seber and LeCren (1967) show that

$$\hat{V}(\hat{N}) = [n_1^2 n_2^2 (n_1 + n_2)]/(n_1 - n_2)^4 \tag{25}$$

$$\hat{V}(\hat{p}) = [n_2(n_1 + n_2)]/n_1^3 \tag{26}$$

Thus, N will be estimated with high precision if $n_1 > n_2$ and n_1 is large and the latter requirement will also ensure an increase in the precision of $\hat{p}$.

Consider an example. Leslie and Davis (1939) estimated the number of rats (*Rattus rattus*) caught during the first, second, and third 2-week periods of a 6-week period during 1937 from an area of 9.1 ha in Freetown, Sierre Leone. The species was regarded as the principal rodent infesting the area. Observations showed that the population was relatively stable and it was reasonable to assume that during the short period of 6 weeks the population was closed.

The data for the first two 2-week periods are $n_1 = 195$ and $n = 119$. Hence from (23) and (25) $\hat{N} = 500$ and $V(\hat{N}) = 5041$ so that the 95% confidence interval for N is 500 ± 142. For a discussion of the general case, see Moran (1951) and Zippin (1956, 1958).

7. Indices

Indices are estimates of animal populations derived from counts of animal signs, road-side counts of breeding birds, and so on. The results do not give estimates of absolute populations, but they do indicate trends in populations from year to year or habitat to habitat.

A number of census methods have been based on ratios calculated from animal signs. If we know the number of signs left by each animal per unit area per unit time, we can calculate the number of animals that must be in the area. A few of the signs that may be used are dens, burrows, nests, tracks, and pellet groups.

Stratified random sample surveys are being annually conducted in the US and Canada for detecting and measuring changes in abundance of non-game breeding birds at the height of the breeding season. The data are collected by volunteer observers who make roadside counts of birds heard or seen on predetermined stops on predetermined routes according to a specified sampling scheme (Robbins and VanVelzen 1967, 1969; Erskine 1970, 1973; Smith 1973). An estimate of change and its error for a particular species between 2 successive years is given by the following:

$$\hat{R} = (\bar{y} - \bar{x})/\bar{x} \tag{27}$$

$$\text{SE}(\hat{R}) = \left(\frac{\bar{y}}{\bar{x}}\right)\left[\frac{[\text{Var}(\bar{y})]}{\bar{y}^2} + \frac{[\text{Var}(\bar{x})]}{\bar{x}^2} - \frac{2\,\text{Cov}(\bar{x},\bar{y})}{\bar{x}\bar{y}}\right]^{1/2} \tag{28}$$

where $\bar{x}$ = mean number of birds/route based on 1st year,
$\bar{y}$ = mean number of birds/route based on 2nd year.

The methods in current use are, however, not sensitive and reliable enough to detect changes for species having highly skewed distributions and based on a smaller number of routes. Sen (1981) discusses these problems and suggests transformation of the basic data to deal with such cases. McClure (1939) describes a census method for Mourning Doves (*Zenaidura macroura*) based on the number cooing in that area. Duvall and Robbins (1952) found a direct relationship between the total number of doves heard and the calls recorded. Kozicky *et al.* (1954) made a statistical study of woodcock songs for 44 routes in northeastern US and suggested a log transformation for efficient analysis of trends. Working on woodcock song data from breeding bird surveys for the Maritime Provinces and Ontario for the 5 years 1973 – 77 on routes ranging from 163 to 220 I found log transformation was not only useful in normalizing the distribution but led to a considerable increase in precision of the estimate of variance of mean songs per route. The estimate of the mean songs per route based on untransformed

data was almost as efficient (90 – 92%) as estimates based on log transformed data. However, direct estimation of the population variance proved very inefficient, the efficiencies ranging between 20 and 25%. This suggested the need for use of transformed data in estimating variance.

Gates and Smith (1972) reported on a theoretical analysis of dove call counts as a means of estimating actual abundance.

7.1. Pellet-group counts

Counting pellet or fecal groups is widely used to estimate big-game populations. The method involves the counting of pellet-groups in sample plots or transects located in the study area. Results of sample counts may be reported simply as the average number of pellet-groups found per unit of area and thus serve only as an index of abundance. In rarer cases pellet-group counts are converted to estimates of actual numbers of animals present on the area sampled.

The accuracy of estimating populations by this method assumes prior knowledge of (*a*) rate of defecation by the animals involved, (*b*) length of the deposition period represented in the samples and also, (*c*) use of efficient sample survey techniques.

Average daily defecation rates may vary among species, with diet, age, and sex of the animal. These were found remarkably constant from day-to-day for deer by Eberhardt and Van Etten (1956) who found "the tendency of missing pellet-groups in sample plots" as the most common source of error; there was also evidence of observer variability in their ability to detect pellet-groups (Ryel 1959). The authors have, however, stated that the above errors can be controlled through use of right sampling procedures, e.g., stratified sampling with proportionate allocation and through intensive training of observers. White and Eberhardt (1980) have discussed procedures for the analysis of this type of data.

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